

Looking forward through the past: identification of 50 priority research questions in palaeoecology

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1 **Looking forward through the past. Identification of fifty priority research**
2 **questions in palaeoecology**

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139 **Running Title:** 50 Priority Research Questions in Palaeoecology

140

141 **Summary**

142 1. Priority question exercises are becoming an increasingly common tool to
143 frame future agendas in conservation and ecological science. They are used to
144 identify research foci that advance the field and that also have high policy and
145 conservation relevance.

146 2. To date there has been no coherent synthesis of key questions and priority
147 research areas for palaeoecology, which combines biological, geological,

- 148 chemical and molecular techniques in order to reconstruct past ecological and
149 environmental systems on timescales from decades to millions of years.
- 150 3. We adapted a well-established methodology to identify 50 priority research
151 questions in palaeoecology. Using a set of criteria designed to identify realistic
152 and achievable research goals, we selected questions from a pool submitted by
153 the international palaeoecology research community and relevant policy
154 practitioners.
- 155 4. The integration of online participation, both before and during the workshop,
156 increased international engagement in question selection.
- 157 5. The questions selected are structured around six themes: human–environment
158 interactions in the Anthropocene; biodiversity, conservation, and novel
159 ecosystems; biodiversity over long timescales; ecosystem processes and
160 biogeochemical cycling; comparing, combining and synthesizing information
161 from multiple records; and new developments in palaeoecology.
- 162 6. Future opportunities in palaeoecology are related to improved incorporation of
163 uncertainty into reconstructions, an enhanced understanding of ecological and
164 evolutionary dynamics and processes, and the continued application of long-
165 term data for better-informed landscape management.
- 166 7. **SYNTHESIS:** Palaeoecology is a vibrant and thriving discipline and these 50
167 priority questions highlight its potential for addressing both pure (e.g.
168 theoretical) and applied (e.g. environmental) research questions related to
169 ecological science and global change.

170

171

172 **Keywords:**

173 Anthropocene; Biodiversity; Conservation; Ecology, Evolution; Human-Environment
174 Interactions; Land-use history; Paleoecology, Palaeoecology; Research Priorities.
175

176

177 **Introduction**

178 Palaeoecology combines biological, geochemical and molecular information from
179 natural archives to reconstruct ecological and evolutionary systems deep into the past.
180 Because ecological monitoring records do not typically extend beyond the past few
181 decades, palaeoecology is key to understanding how ecosystems have responded to
182 past disturbance, evaluating their resilience to perturbations, and defining their pre-
183 anthropogenic variability (Jackson 2007; Willis *et al.* 2010). High-resolution sediment
184 sequences, for example, were pivotal in assessing the timing and extent of lake
185 acidification across large areas of northern Europe and North America in the 1980s,
186 and for attributing the cause to acidifying compounds derived from the combustion of
187 fossil fuels since the Industrial Revolution (Battarbee *et al.* 2010). Today, European
188 legislation such as the Water Framework Directive (WFD) requires assessment of
189 ecological quality in relation to pre-anthropogenic baselines. Palaeoecology has been
190 demonstrated to be the best approach to provide objective information about past
191 conditions (Bennion *et al.* 2010).

192

193 Long-term insights are also crucial for identifying and understanding ecological and
194 evolutionary processes. From around 50,000 years ago, a disproportionate amount of
195 large-bodied mammals and birds (megafauna) began to go extinct in Eurasia,
196 Australia and the Americas (Barnosky 2004). Accurately dated chronologies of the
197 Pleistocene fossils have allowed the timing and potential causes of these megafaunal
198 extinctions to be constrained (Burney & Flannery 2005). In addition, they have
199 demonstrated that the loss of large herbivores led to the formation of novel
200 ecosystems (Gill *et al.* 2009) and resulted in major changes in vegetation composition

and fire regimes (Rule *et al.* 2012). In this case the integrated analysis of palaeoecological records revealed the unexpected legacies of extinction events on ecosystem functioning; this cannot be accomplished by studying modern systems alone.

But what are the future important questions that palaeoecological studies could and should be addressing? This paper describes the results from an exercise to identify 50 priority research questions in palaeoecology. This was inspired by previous studies, which have used specific criteria to identify priority research questions to advance the field of a given discipline (Sutherland *et al.* 2009; Pretty *et al.* 2010; Sutherland *et al.* 2011; Grierson *et al.* 2011; Petrokofsky, Brown & Hemery 2012; Sutherland *et al.* 2013; Walzer *et al.* 2013). Here we present the results of a two-day workshop held at the Biodiversity Institute, University of Oxford, in December 2012 and describe both the empirical (e.g. ecological and evolutionary, methodological) and applied research questions (e.g. environmental and conservation) on timescales covering decades to millions of years.

Materials and methods

We adapted the methodology of Sutherland *et al.* (2011) to incorporate an open application process and online voting over the course of the workshop. We asked individuals to identify their top priority questions in various branches of palaeoecological science (see Supporting Information 1). Prior to the workshop, 905 questions were submitted online from 127 individuals, laboratories and organisations, which spanned 26 countries and five continents. Workshop coordinators [AWRS, AWM, AGB] pre-screened the submitted questions for duplication, which resulted in

804 questions organised into 55 topics. The questions were then selected and refined through an iterative process of voting and reworking using a simple scoring system (0, zero priority; 1, low priority; 2, high priority) (Fig. 1). All participants are listed as co-authors above. Questions are identified in the text by reference to their number [Q1] and are not ranked but are grouped thematically, both between and within working groups.

Results

Human-environment interactions in the Anthropocene

1. When did human activities first trigger global environmental change and can we define the start of the Anthropocene with reference to these activities?
2. How did changes in human livelihood, settlement strategies and land-use affect land cover, ecosystem structure, nutrient cycles, and climate over the late-Quaternary?
3. Why are some species and ecosystems more sensitive to environmental change than others, and therefore respond first or to the greatest degree?
4. Why do different species and ecosystems experience varying time-lags in their response to environmental change?
5. What effect has Holocene landscape fragmentation had on the ability of natural and semi-natural vegetation types to respond to environmental change?
6. How can the relationships between climate, herbivory, fire and humans be disentangled?
7. What are the impacts of pollutants on biota, including contaminants of emerging concern and their interactions with other stressors?

It has long been known that combustion of fossil fuels pollutes the Earth's atmosphere. The concept of the Anthropocene recognises that human activity has now transformed many of the Earth's ecosystems on a global scale (Crutzen & Stoermer 2000), yet formalizing the Anthropocene as a new geological epoch remains controversial (Zalasiewicz *et al.* 2011; Gibbard & Walker 2013). One debate surrounds whether it began at the onset of the Industrial Revolution, or thousands of years earlier following the expansion of agriculture and concomitant increases in atmospheric CO₂ and CH₄ (Ruddiman 2012). An important future challenge for palaeoecologists is to understand the timing of impact [Q1] and how ecosystems responded in these human mediated landscapes [Q2-6].

The broad theme of human-environment interactions was identified as an area where a strong overlap exists between ecological and palaeoecological research (see, e.g., Sutherland *et al.* 2013). However, an additional challenge identified by palaeoecologists concerned the threats posed by new and emerging pollutants, especially when interactions with other stressors such as climate change were considered (Noyes *et al.* 2009; Murray, Thomas & Bodour 2010) [Q7]. For example, widespread application on boats of antifouling tributyltin (TBT) in the Norfolk Broads resulted in the decline in grazing organisms and subsequent proliferation of phytoplankton, which led to the collapse in aquatic macrophyte communities (Sayer *et al.* 2006) (Fig. 2). Palaeoecological records were vital in identifying major changes in ecosystem structure and function representing regime shifts, and have much to offer in disentangling the drivers and impacts of these stressors.

Biodiversity, conservation and novel ecosystems

- 276 8. In the context of global change and cultural landscapes, is the concept of
277 natural variability more useful than baselines in informing management
278 targets, and, if so, how can it be defined and measured in the palaeorecord?
- 279 9. How can palaeoecological data be used to inform ecosystem restoration,
280 species recovery and reintroductions?
- 281 10. How can the palaeoecological record be applied to understand the interactions
282 of native, alien and invasive species?
- 283 11. How can palaeoecology help define, characterize, and inform the management
284 of novel ecosystems?
- 285 12. How can palaeoecology be applied to characterize the dynamics of ecosystem
286 services?
- 287 13. How should palaeoecological results be translated and communicated
288 effectively to ensure they are adaptively integrated into environmental
289 strategies for the present and future?
- 290 14. What are the legacies of past environmental changes on the current structure,
291 resilience and dynamics of natural and socio-ecological systems?
- 292 15. Which factors make some systems more resilient to environmental change
293 than others?
- 294 16. Can palaeoecological records provide improved insight into the theory, causes,
295 consequences and modelling of critical transitions and alternative stable
296 states?
- 297 17. What can palaeoecology reveal about early warning signals of abrupt change?
298

299 Successful conservation and management of ecosystems requires knowledge of long-
300 term change and variability. Several biodiversity intactness indices, for example,

301 require knowledge of a ‘baseline’ ecological state (Scholes & Biggs 2005; Nielsen *et*
302 *al.* 2007), but this fundamental information is often cited as a ‘key deficiency’ or
303 knowledge gap (The Royal Society 2003; Froyd & Willis 2008). Furthermore, in
304 novel ecosystems or in those that have experienced very rapid change or species
305 reshuffling, a return to baseline conditions may not be achievable or even appropriate
306 (Hobbs *et al.* 2006). ‘Conservation paleobiology’ is emerging as a discipline to
307 address the challenges of using long-term data to inform restoration and management
308 (Dietl & Flessa 2011). Important questions to be answered in the future include
309 assessing the degree of change from specified historical ecosystems (Fluin *et al.* 2007;
310 Gillson & Duffin 2007); [Q8]; the viability and level of intervention required to
311 restore such historic conditions where desirable (van Leeuwen *et al.* 2008) [Q9, 10];
312 the extent of human influence and the management of cultural landscapes (Chambers
313 *et al.* 2013; Shaw & White 2013) [Q8, 9, 11]; and identifying and guiding
314 conservation of emerging novel ecosystems in order to maintain ecosystem services
315 (Jackson & Hobbs 2009) [Q11, 12]. Promoting and communicating palaeoecological
316 data in conservation planning could also play an important role in informing
317 ecosystem management [Q13].

318 Resilience theory has also becoming an influential framework in landscape
319 management due to its potential for understanding ecological change in complex
320 systems. The theory highlights the importance of identifying slow variables (i.e.
321 processes occurring over decadal- centennial timescales or longer) that can lead to
322 transitions between alternative stable states (Holling 1973; Scheffer & Carpenter
323 2003). For example, the relationship between resilience, environmental change, and
324 political dynasties was explored by Dearing (2008) in the Erhai lake-catchment in
325 Yunnan Province, China (Fig. 3). Analysis of lake sediment and historical records

showed that agricultural expansion ~1400 cal yr BP initiated widespread gullying that continued for ~600 years. These long-term records revealed the possibility of alternate steady states in the catchment, and suggested that the landscape was characterized by low resilience today. Identifying critical thresholds and predicting when they might be crossed has been highlighted as a priority research area in ecology (Scheffer & Carpenter 2003; Sutherland *et al.* 2013) and one where palaeoecology has the potential to provide many exciting insights [Q14-17].

Biodiversity over long timescales

18. What is the role of sea-level change in community and diversity dynamics through time and across marine and terrestrial environments?

19. What drives the spatial expansion and contraction of a species over its duration?

20. At what rates have species ranges shifted during past intervals of climate change, and what geophysical factors, biological traits and their interactions have affected these rates?

21. How can the rate and spatial dynamics of extinctions in the fossil record, together with palaeoclimate modelling, help in predicting future ecological and biodiversity loss?

22. Why do the co-occurrences of some species persist through time? Is the stability of these associations caused by similar environmental niches, co-evolutionary relationships, or randomness?

23. What processes control the stability/variability of realized and fundamental niches through time?

24. How has varying atmospheric composition shaped biotic interactions (e.g., between C3 and C4 plants, trees and grasses, megaherbivores and forage, insects and plants)?

25. What are the appropriate null models in palaeoecology for testing hypotheses about ecological and evolutionary processes?

Biodiversity dynamics are primarily regulated through the interaction of speciation and extinction rates through time. Molecular phylogenies on extant taxa are limited in that they typically only provide insights into the speciation process. In contrast, palaeoecological records can be used to track the waxing and waning of a species, and in some cases (e.g. Cenozoic planktonic foraminifera) the record can be interpreted as a single line of descent that begins with speciation and ends in extinction (Simpson 1962). One important consideration is the abiotic processes (including, but not limited to, temperature) influencing diversification rates. Sea-level variations throughout the Phanerozoic, for example, are likely to have had major influences on the evolutionary trajectories of different species through reproductive isolation and speciation. Sea-level changes may also influence evolutionary processes by increasing chances of dispersal and changing habitat type (Abe & Lieberman 2009). Similarly, environmental instability early on in a species' lifespan has been shown to influence species' persistence over time (Liow *et al.* 2010) but what is still poorly understood is the rate and driving mechanisms of this process [Q18,19]. On shorter timescales, changes in climate on glacial-interglacial cycles have also been demonstrated to influence migration rates, dispersal and range size changes (Bennett 1997). Understanding how these environmental variables influence geographic range and niche dynamics is essential as geographic range directly impacts on the extinction risk

of species. This is an area of research where palaeoecology has much to offer [Q20, 21, 23].

Biotic interactions can also shape evolutionary processes. Whilst the Quaternary record shows constant turnover of communities and development of novel ecosystems, particularly at times of rapid climate change, on deeper timescales the persistence of some species, especially plants, is remarkable (Willis and McElwain 2014). This leads to the question of which factors lead to long-term persistence [Q22] and the challenges of quantifying the interplay between abiotic change and biotic interactions (Ezard *et al.* 2011). A classic example of this is the relationship between C3 and C4 plants from the Oligocene (approx. 33 Ma); how this biotic interaction was influenced by changing atmospheric CO₂ concentrations and aridity is still poorly understood (Strömberg 2011) [Q24].

Interestingly, a question on ‘null models’ [Q25] emerged in the priority list. Null models use permutation procedures on ecological data in order to produce a distribution that would be expected in the absence of a particular ecological mechanism (Gotelli & Graves 1996). Although null models have played a particularly important role for explaining patterns of dispersal (Hubbell 2001), this approach is fundamental to all scientific disciplines and yet is rarely considered.

Ecosystem processes and biogeochemical cycling

26. How have terrestrial carbon, nitrogen and silica cycles been linked in the past, specifically at times of abrupt climate change?

- 399 27. What was the effect of centennial-scale climate variability on the carbon
400 balance of terrestrial and aquatic ecosystems at regional to global scales?
- 401 28. How can palaeoecological data from continental shelf areas help characterise
402 anthropogenic impacts on geochemical fluxes (e.g. silica, C, N and P) from
403 land to shallow marine ecosystems during the Holocene?
- 404 29. How does species turnover (e.g. immigrations, extinctions) and varying
405 community composition affect ecosystem function, including carbon
406 sequestration?
- 407 30. How can sedimentary records be used to address process-based questions and
408 to test mechanistic ecological models so as to provide insights about the past
409 functioning of ecological systems?
- 410 31. How can ecological interactions (e.g. competition, predation, mutualism,
411 commensalism) and their possible evolutionary consequences be inferred from
412 palaeoecological data?
- 413 32. How can disturbances such as insect outbreaks or pathogens be detected in
414 palaeoecological data?
- 415 33. What are the taphonomic characteristics of ancient DNA, in particular under
416 different climatic and sedimentary contexts?

417

418 Ecological systems are linked with the abiotic environment through fluxes of energy
419 and matter. Therefore, quantifying the rate and magnitude of the biogeochemical
420 cycling of different nutrients, and how these rates respond to different stressors, is
421 fundamental to understanding how an ecosystem functions and something that
422 palaeoecological science can help address [Q26-29]. The uptake of carbon by
423 terrestrial ecosystems, for example, is limited by N availability (Mitchell and

424 Chandler in Sokolov et al. 2008). A key question for global change ecologists
425 involves understanding how these two cycles will co-vary in the future, particularly in
426 the context of increasing carbon dioxide concentrations and excess nitrogen
427 deposition (Galloway & Cowling 2002) [Q27]. The utility of this approach has
428 recently been demonstrated in an integrated palaeoecological study from 86 sites
429 globally. This revealed the slow response of the global N cycle relative to major
430 changes in CO₂ during the glacial-interglacial transition (McLauchlan *et al.* 2013).
431 Overall, a decline in N availability was observed between 15,000 and 7,500 years ago
432 (declining values of $\delta^{15}\text{N}$), with no net change in global sedimentary N availability
433 observed in the past 500 years (Fig. 4). This result was surprising, since one might
434 expect an increase in sedimentary $\delta^{15}\text{N}$ following the excess N input into systems at
435 this time. Such studies highlight the important role that palaeoecology can play in
436 understanding ecological functioning, particularly at times of abrupt climate change.
437
438 In ecological research, problems involving complex trophic interactions,
439 biogeochemical cycling and population dynamics are often addressed using process-
440 based models [Q30-31]. This represents an exciting area of palaeoecological research,
441 particularly for understanding demographic effects and biotic interactions (Jeffers *et*
442 *al.* 2011). Similar approaches might also be applied in, for example, research
443 concerning pest-pathogen outbreaks, for which reliable detection methods are still
444 required [Q32]. Finally, major ecological insights can be gained from understanding
445 changes in genetic variability of populations through the recovery and study of
446 ancient DNA (aDNA) from fossil remains. A remaining technical challenge in this
447 research area concerns the understanding of taphonomic processes influencing aDNA
448 preservation [33] (e.g. Haile *et al.* 2007).

Comparing, combining and synthesizing information from multiple records

34. What methods can be used to develop more robust quantitative palaeoenvironmental reconstructions and ensure reliable estimates of the associated uncertainties?
35. How can palaeoecologists disentangle the separate and combined effects of multiple causal factors in palaeoecological records?
36. When using modern analogues, what measures can be taken to be sure that the training set is sufficient to reconstruct the full range of likely past conditions, and if not, what else should be used to supplement these methods?
37. What methods can be used to identify and quantify the effect of diagenetic and taphonomic processes on the palaeoecological record?
38. How does taxonomic and numerical resolution affect the recognition of community, metacommunity, and other ecological patterns?
39. How can common environmental signals be identified in multiple records at different spatial and temporal scales?
40. What methods can be used to better assess the leads, lags, and synchronicities in palaeorecords at different spatial scales?
41. Given that palaeoecology relies on accurately dated chronologies, how can the often incompatible dates derived from different dating techniques (e.g. ^{210}Pb & ^{14}C , ^{14}C & OSL) be reconciled to improve the dating of key time periods (e.g. the Industrial period; MIS 3)?

Modern research in palaeoecology focuses both on understanding the ecology and environment of single geographical locations (via, for example, analysis of lake, peat, ocean and ice core records) and on reconstructing past environments and ecosystems at regional, continental and global scales. While tools for single-site analysis have been evolving since the earliest work in palaeoecology (e.g. Fægri & Iversen 1950), tools for inter-site comparison and regional synthesis are relatively undeveloped and face two main challenges. The first is to disentangle the effects of multiple causal factors on palaeoecological records at single sites and across multi-site networks (Cunningham *et al.* 2013; Juggins 2013). The second is to quantify the sources of uncertainty that accumulate as one moves through the causal chain that links climate or other environmental drivers to the palaeoecological observations (Fig. 5).

There are many sources of uncertainty in palaeoecology. Some relate simply to the stochasticity of the natural world, but others arise because of the often indirect link between the palaeoenvironment and the observations obtained. For example, palaeoecological records typically comprise multi-species assemblages from multiple biological groups (Birks & Birks 2006) that are preserved in long environmental archives that experience complex post-depositional processes (Birks & Birks 1980). The transfer function methods used to quantify the relationship between ecological assemblage and climate are already used to formalise some of the links in the causal chain from palaeoenvironment to field and lab observations (e.g. Haslett *et al.* 2006). However, such explicitly causal models are rare and many such links are simply described qualitatively and not formally modelled. Five questions draw attention to these issues in general or as they relate to specific links in the causal chain [Q34-38].

An additional challenge involves the synthesis of information from multiple sites [Q39-41]. For such projects issues of chronology often become a primary focus since, unless the records to be combined are on a comparable time scale (with reliable estimates of uncertainties), robust synthesis is impossible (Blaauw & Heegaard 2012). There is a need to improve existing and develop new chronological techniques, and to understand and reconcile the differences observed between the chronologies derived from different techniques (e.g. Piotrowska *et al.* 2010; Blockley *et al.* 2012). The need to develop new methods for dating 19th century sediments is seen as a particular priority (e.g. see Rose & Appleby 2005). This time period is increasingly beyond the range of ²¹⁰Pb dating and as the gap between conventional ¹⁴C and ²¹⁰Pb dating becomes progressively greater, novel dating techniques such as ³²Si hold great potential (Morgenstern *et al.* 2013) [Q41].

Developments in palaeoecology

42. Do ecological principles, formulated to account for present day (10-100 years) patterns, hold when applied to palaeoecological patterns (>100-1000 years), or are there palaeoecologically important ecological processes that are impossible to study with modern observational data?
43. What common questions can be addressed by ecologists and palaeoecologists to bridge the contrasting spatial and temporal scales between the two disciplines effectively?
44. How can palaeoecological records contribute to and advance key concepts that are currently central to ecological thinking, including model comparison and stochastic process modeling?

45. How can forest inventory data, modern pollen databases, and pollen loading equations be integrated effectively to facilitate the generation of robust estimates of tree and land cover?
46. How best can palaeoecologists create an accessible, consistent, usable and future-proof record of historical and archaeological sources integrated with contemporary ecological observations?
47. What new opportunities and research agendas, arising from the availability of higher spatial, temporal and taxonomic resolution data, will be created with the adoption of automated counting systems for microfossils?
48. What are the developmental and genetic controls on morphology, and how can the fossil record be used to study phenotypic plasticity and the evolution of developmental systems?
49. How do palaeoecologists encourage hypothesis testing rather than data-dredging approaches when exploring relationships between proxies and records?
50. How can closer collaboration between palaeoecologists and statisticians be fostered in order to ensure development and dissemination of appropriate statistical techniques?

In the last three decades, palaeoecology has been transformed from a discipline dominated by studies on the composition and structure of fossil assemblages preserved in sediments (e.g. Birks & Birks 1980) into a sophisticated multi-disciplinary science involving not only palaeobotany, palaeozoology and archaeology, but also inorganic and organic geochemistry, stable-isotope assays, geochronology, dendrochronology, aDNA studies, modelling and applied statistics (Flessa & Jackson

2005; Birks 2008). Here, two outstanding developments were identified. New identification and counting systems (Holt *et al.* 2011; Punyasena *et al.* 2012) and multivariate morphometric techniques (Claude 2008) [47] have the potential to investigate morphological variability observed in the fossil record in detail. For example, when combined with aDNA techniques [Q33], these new tools could be used to investigate whether genotypic changes can be disentangled from phenotypic shifts [48]. The second involves the fast emerging discipline of palaeoecoinformatics (Brewer, Jackson & Williams 2012), which is encouraging open-access databases of palaeoecological data (e.g. Neotoma 2013). Rigorous data standardization of both fossil and modern pollen is essential in data-synthesis. Data-mining exercises could be used to provide more reliable reconstructions of species dynamics, vegetation composition and landscape structure in space and time [Q45, 46].

But despite these new developments, some fundamental principles remain to be answered. Thus, the importance of the essential links between palaeoecology and ecology was emphasised, with a focus on integrating data across spatial, taxonomic and temporal scales (e.g. Gray 2004; Helama *et al.* 2010) [Q42-44]. Finally, three questions were targeted at challenging the research approaches of palaeoecologists themselves. There is an increasing need to exploit the full potential of dynamic modelling, quantitative model comparison and statistical hypothesis-testing in palaeoecological analyses (Jeffers *et al.* 2011; 2012) [Q44, 49] so as to provide a rigorous basis for further quantitative analytical approaches in palaeoecology (Birks 1985; Birks 2012) [see also Q25]. This requires close collaboration between palaeoecologists, ecological modellers, and applied statisticians [Q50].

573

574 **Discussion**

575 Evaluation

576 Our study follows other priority research exercises in, for example, ecology, applied
577 ecology and conservation science (Sutherland *et al.* 2006; Sutherland *et al.* 2009;
578 2013). All of these exercises are dependent on the individual skills, interests and
579 expertise of the participants and our questions do not, therefore, represent a definitive
580 list. We also noted that whilst the 804 screened questions were a mixture of both
581 general and specific, questions became increasingly general through subsequent
582 iterations. More than 100 questions involving pollen analysis were submitted, for
583 example, but these were translated into more general questions that could be applied
584 to multiple proxy groups or habitat types. The end result is a list of questions that can
585 be tailored to a variety of research problems.

586

587 As an example, a widespread decline of *Tsuga canadensis* (Eastern hemlock) is
588 observed in fossil pollen records ca. 5,500 cal yr BP across its entire range in eastern
589 North America. Its drivers have been ascribed to climate (Shuman, Newby &
590 Donnelly 2009), a pest-pathogen outbreak (Davis 1981), or a combination of the two
591 (e.g. Booth *et al.* 2012). Whilst there is some evidence for fossil head capsules of
592 insect pests found in limited sites around the time of the decline (Bhiry & Filion
593 1996), evidence for a range-wide outbreak remains inconclusive. Thus, one obvious
594 important development is to find new ways of detecting pest-pathogen outbreaks in
595 the palaeoecological record [Q32]. Additional information could be inferred using
596 process-based models to infer population dynamics [Q31, 44]. If the hemlock decline
597 was driven by climate, then an additional question would be why this species

responded more sensitively than others [Q3], or whether it was the result of cross-scale interactions between climate and the pathogen, or the interactions of multiple stressors [Q35, 39]. Thorough testing of the problem also requires integrating multiple palaeoecological sites [Q39]. Even the timing and synchrony of the hemlock decline is now being debated so resolving age uncertainties between pollen and other climate records is vital [Q40].

Looking forward

This exercise also provided an opportunity to reflect on the status of the discipline today. How do our questions compare to those identified in fundamental ecology and what can we infer about the future directions? Von Post's seminal work in the early 20th century was heavily focused on describing patterns of vegetation change as a relative dating tool over the past 11,000 years. There was little consideration of the underlying ecological mechanisms responsible for the observed changes. In contrast, from the 1980s onwards, many fossil pollen data-sets were developed specifically to reconstruct past climate change with little attention given to the patterns of vegetation change. In these studies quantification and reconstructions of single sites was a key focus, whilst there were a growing number of studies that were being applied to test ecological hypotheses.

The questions identified in this study highlight a different situation for modern palaeoecological science. Only 8% of the initial questions submitted to the website were specifically targeted at filling data gaps, or represented a specific regional study. None of these were selected in the final question list. Instead, topics covered included community, species and diversity dynamics (18%); ecosystem functioning (12%);

global change ecology and human impacts (18%); and ecosystem management (12%).

Therefore, primarily through its ability understand ecological responses to environmental change, the perceived disconnect between neo-ecology and palaeoecology that has been reported in the past is being eroded (see, e.g. Froyd & Willis 2008). As a result, common themes between these questions and those in the recent fundamental ecology exercise (Sutherland *et al.* 2013) can be identified. Examples include factors that control species range shifts; biogeochemical cycling under rapid climate change; and measuring and quantifying ecological resilience. This suggests that there is great potential for further integration between the two sub-disciplines.

One other striking feature of the 50 questions is the heavy dependence on methods. 40% of the questions were related to methodology, either directly by focusing upon improved precision and accuracy, or by finding new ways to apply and interpret palaeoecological data to address broader questions of, for example, landscape management. In palaeoecological research this is not surprising. Proxy data are indirect measures of a targeted environmental variable, whilst robust palaeoecological inferences are also heavily dependent on indirect dating techniques. This is in contrast to, for example, neo-ecology, in which the ecological units of analysis can often be directly observed. This result does not undermine the capability of palaeoecology to provide long-term insights. It does, however, highlight the continued rigour in the discipline and widespread acknowledgement of the importance of understanding what proxy data can and cannot tell us. A major focus for the future then, will remain in characterizing the uncertainties between target variable and proxy source to make robust ecological and evolutionary inferences (e.g. Jackson 2012) (Fig. 5).

648

649 The questions selected also hint at cross cutting themes that have the potential to
650 influence palaeoecological research in the future. The move from site-specific
651 descriptions towards addressing global scale issues, for example, is reliant on
652 upscaling and comparing multiple records. This will require efficient data
653 management techniques that are able to compare and correlate multiple proxies. A
654 second cross-cutting theme involves disentangling the synergistic effects of multiple
655 variables (e.g. fire, human impact, faunal composition). We now realise that
656 ecosystems represent complex systems, experiencing chaotic fluctuations and
657 alternative stable states, and these dynamics partially explain the unpredictable
658 ecosystem responses following an extrinsic forcing. Finally, there are a number of
659 questions that highlight the importance of biotic interactions. Better characterization
660 of these in palaeoecological records may also improve our understanding of
661 community dynamics in complex systems.

662

663 In summary, the 50 questions identified and discussed in this paper highlight the
664 potential for palaeoecology to address both empirical and applied research questions
665 related to ecological science and global change. These questions demonstrate the
666 critical importance of historical context in understanding the Earth system and, whilst
667 we do not claim that they are definitive, they outline key areas in the future
668 palaeoecological research agenda.

669

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FIGURES

Figure 1. Schematic showing the pre-screening process followed by workshop structure used to reduce 905 submitted questions to the final 50 priority questions.

Figure 2. (from Sayer *et al.* 2006). Summary butyltin (μ g-1) profiles and biostratigraphy for a sediment core from Hickling Broad. Macrofossil data are expressed as a flux (no. cm² yr⁻¹) to account for differential rates of sediment accumulation over the core profile. Palaeoecological data was used to identify a regime shift in aquatic communities following exposure to pollutant stressors.

Figure 3. (from Dearing 2008). Landscape stability in alternative steady states from the Lake Erhai basin, China. Two ‘steady’ states can be identified from assessing the relationship between soil erosion rates and the % of non-arboreal pollen. A non-degraded state between 2960–1430 cal yr BP, 600 yr transition period, and a degraded state between 800 cal yr BP and the present. This example demonstrates the value of palaeoecological data for testing attributes of resilience theory and for better understanding complex system dynamics.

Figure 4. (from MacLaughlan *et al.* 2013). Changes in lacustrine sedimentary $d^{15}N$ during the late Pleistocene and Holocene. The $d^{15}N$ record is a proxy for nitrogen availability, with higher ^{15}N values occurring when N supply is high relative to biotic

demand. Palaeoecological evidence revealed both the slow response of the nitrogen cycle to major changes in CO₂ and temperature over the glacial-interglacial transition; and no net change in N demand over the past 500 years. This is surprising since there has been doubling of the pre-industrial supply of nitrogen in the past 200 years, and reveals the important long-term of net terrestrial C balance in maintaining global biogeochemical cycles. A) A smoothing spline curve (0.05 smoothing parameter) fitted to the means of sites in 100-yr bins is shown (red) with 95% bootstrapped confidence intervals (grey). Declines in sedimentary d¹⁵N from 15,000 cal. yr BP to the breakpoint at 7,056 ± 597 cal. yr BP correspond with periods of global net terrestrial carbon gain (shaded green). Dotted black line is the breakpoint regression. B) A different set of high-resolution sedimentary d¹⁵N records shows no net change over the past 500 yr.

Figure 5. (from Jackson 2012) A general conceptual model for representation of vegetational, biogeographic, or other entities in paleoecological records. The target is the primary entity of interest, and the inference is the end point in the chain. Each oval represents a series of processes by which information is transferred and transformed, and each process is accompanied by distinct uncertainties, distortions, and loss of information. The aim is to ensure that properties of the final inference will correspond to those of the original target (i.e., reality). However, the inference is usually accompanied by substantial uncertainty accumulated along the chain.